HIDE AND GO SEEK: WHAT DOES PRESENCE MEAN IN THE FOSSIL RECORD?

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Abstract

Our efforts to reconstruct accurate, complete records of events in vegetation history and in plant evolutionary history depend on accuracy in dating sediments, interpretation of structures preserved, reconstruction of whole organisms or communities from the preserved material, and interpretation of the interaction between past abundance and fossil presence. This contribution examines the interaction between past abundance of a target plant and the probability of retrieval of that species in the fossil record. By examining records of recolonization in volcanic areas, records of invasive species spread, succession in disturbed habitats, and historical migration patterns, we can provide estimates of the likelihood of appearance in the potential fossil record of newly evolved and reasonably successful species. The lag in discovery, recognition, and publication of a fossil as an important representative of a critical clade is also evaluated and is highlighted as a more important constraint on the use of fossils in testing evolutionary and ecological hypotheses than the recolonization rate. The lag between discovery and publication is particularly relevant in areas of the modern world where fossil plant–bearing deposits are either rare or inaccessible. Greater awareness of the density and reliability of the plant record should allow evolutionary biologists and paleoecologists to bracket not only time intervals but also geographic regions where the fossil record can be interpreted largely at face value. At the same time, more effort should be focused on intense collecting efforts and training in areas where fossil deposits are potentially present, but poorly collected and evaluated.

Key words: Invasive species, paleobotany, plant evolution, stratigraphic resolution, taphonomy.

The fossil record has a pivotal role in retelling the story of plant evolution. Research into the molecular basis for development of plant organs and the application of DNA amplification and sequencing techniques to outline plant phylogenies interfaces with direct evidence from the fossil record. The fossil record has the potential to place time constraints on models of lineage evolution, diversification, specific morphological traits and combinations, as well as to clarify the longevity of both traits and characters (Rothwell, 1999; Frohlich & Parker, 2000; Magallón & Sanderson, 2001; Pryer et al., 2001; Crepet et al., 2004; Davies et al., 2004; Soltis & Soltis, 2004; Anderson et al., 2005).

These new and exciting applications require increased rigor and specificity from our reading of the fossil plant record. Era-level dates, formation-level stratigraphic placements, and nonquantitative descriptions and reconstructions are no longer sufficient. Similarly, superficial readings of the paleontological literature are no longer likely to adequately test evolutionary hypotheses. Original provenance of the plants in a community, as well as the current and past location of the geological crust on which they are deposited, have become much more important in research on plants in the geological record.

However, a caveat can almost always be raised: the fossil record is incomplete. Ecological and evolutionary processes often operate over short time intervals, and, therefore, the incomplete fossil record is best used with, or even replaced by, other types of data. So what should the interpretation be when, at arm's length, the fossil record indicates that many of the significant and defining features of the angiosperms appeared virtually simultaneously (Darwin, 1903; Crane et al., 1995; Magallón et al., 1999; Crepet, 2000; Anderson et al., 2005; Davis et al., 2005; Friis et al., 2006)? Even when the sequence of phylogenetic events is addressed at a finer scale, such as within angiosperm subgroups (Saxifragales, Malpighiales), the density of fossil data and molecular analyses available point to the rapid evolution of currently diverse and widespread lineages in the Albian and Cenomanian (Fishbein et al., 2001; Davis et al., 2005). With these relatively well-constrained studies, confidence intervals on individual branching events can range from seven to 28 million years. In some cases, fossil evidence applied to dating molecularly based phylogenies rests on a single occurrence of a

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single plant organ from few sedimentary outcrops (e.g., Wikström et al., 2001; Bremer et al., 2004; Crayn et al., 2006). While we should take seriously the verified presence of a taxon as excellent data, regardless of its uniqueness, neither the absence of a lineage nor the gap between occurrences is typically so carefully weighed. This biased approach to the fossil record is analogous to a hypothetical example of a molecular biologist extracting DNA from a 1 × 1 cm piece of tissue from a single mature leaf from a single forest in Thailand and characterizing the phylogenetic position of an entire family of angiosperms based on a sequence of 850 bp from that leaf. More data are potentially available, but for logistical reasons they just are not collected, processed, and applied.

Treatment of the obvious gaps in the fossil record can take two routes. Either gaps are ignored, reporting only what we know now, or gaps are acknowledged and the weakness of the record highlighted as an area for future research. The second route does not need to declare defeat but, rather, to state the uncertainty associated with the lack of sequential, consistent fossil occurrences. A parallel situation occurs with the enthusiastic reports of increased crop yield from radically elevated CO_2 concentrations based on small enclosures. The conclusion is that increased CO_2 may be a positive result for humans. Simultaneously, however, open-grown crop plants in elevated CO_2 sites (Free Air CO_2 Enrichment [FACE]) are only marginally higher than in control sites (Long et al., 2006). Knowledge of the data from open field experiments fills a gap that otherwise would provide for misplaced optimism under increased CO_2 for crop yields (Tubiello et al., 2007). In a similar fashion, this contribution is intended to focus attention on the gaps in the fossil record as a means of encouraging investigations that will improve our understanding of the limits of those gaps.

An outline of the events relevant to fossilization of plants is first presented, starting with the evolution of a new species and ending with the use of that fossil species in a phylogenetic or morpho-developmental context (Fig. 1). Each step involves some modification of the original abundance, morphology, and likelihood of recovery of the plant species. Each has the potential to distort subsequent interpretations. The uncertainty introduced by each step in this chain of events should theoretically be quantifiable and, thus, provide us with an estimate of potential error. Two of these steps are highlighted (bold print, Fig. 1) in the remainder of this contribution, relative to their importance in interpretation of the quality of the reported fossil record.

Steps in the fossilization of fossil plants have been addressed particularly carefully by Spicer (1981), Scheihing and Pfefferkorn (1984), Ferguson (1985), Gastaldo et al. (1987), Gastaldo (1988, 1994), Burnham (1989, 1993), Greenwood (1991), Burnham et al. (1992), and van der Burgh (1994). In each of these studies, the steps in the fossilization process are outlined for slightly different reasons, and thus slightly different interpretations emerge. A frequent casualty of the fossilization process is the qualitative and quantitative correspondence between the source forest and the plant debris incorporated into the fossil record. As fossilization proceeds, selective bias toward thicker and more abundant leaves most often results, even if these are not the most common in the source forests. In addition, small-statured species (herbs, shrubs, lianas) are reduced in abundance, relative to large-statured species like trees (Scheihing, 1980; Burnham, 1997). Furthermore, species with distinctive and well-preserved morphological features are most readily identified by paleobotanists, and species with a preference for moist, soggy, lacustrine, or riparian habitats are favored during fossilization over those with high abundance in dry or mesic habitats (Greb et al., 2006). These are important aspects of interpreting the fossil record, and prior studies have suggested the number of specimens needed for accurate interpretations, the environments most likely to preserve an accurate record of the paleovegetation, and the effect of differential degradation of plant species and plant organs.

This set of steps, from the first ecological and evolutionary appearance of a plant group to its use by humans in describing evolutionary history, is a critical pathway in interpretation and fidelity of the fossil record. Each factor can vary with geographic region, climatic regime, type and continuity of sedimentation, plant habit and abundance, and distinctiveness of the species. Any blanket statements about the character of the fossil plant record and its fidelity are clearly distillations of the variability inherent in the fossil record. In general, if the fossil plant record is to be used most reliably, records should be based on large-bodied, abundant, perennial wetland species, whose reproduction is frequent and includes both sexual and asexual reproductive organs. Even so, we should expect large gaps in the fossil record due to periodic loss of habitat, lack of sedimentation, and erosional activity.

Two fossilization steps are addressed here (Fig. 1) to clarify the constraints and advantages of applying the plant fossil record to evolutionary history. First addressed is **abundance increase** (increase in population density and extent), which asks the question: how long does it take from simple presence as a species to abundance of the species with biomass large enough to have a high likelihood of represen-

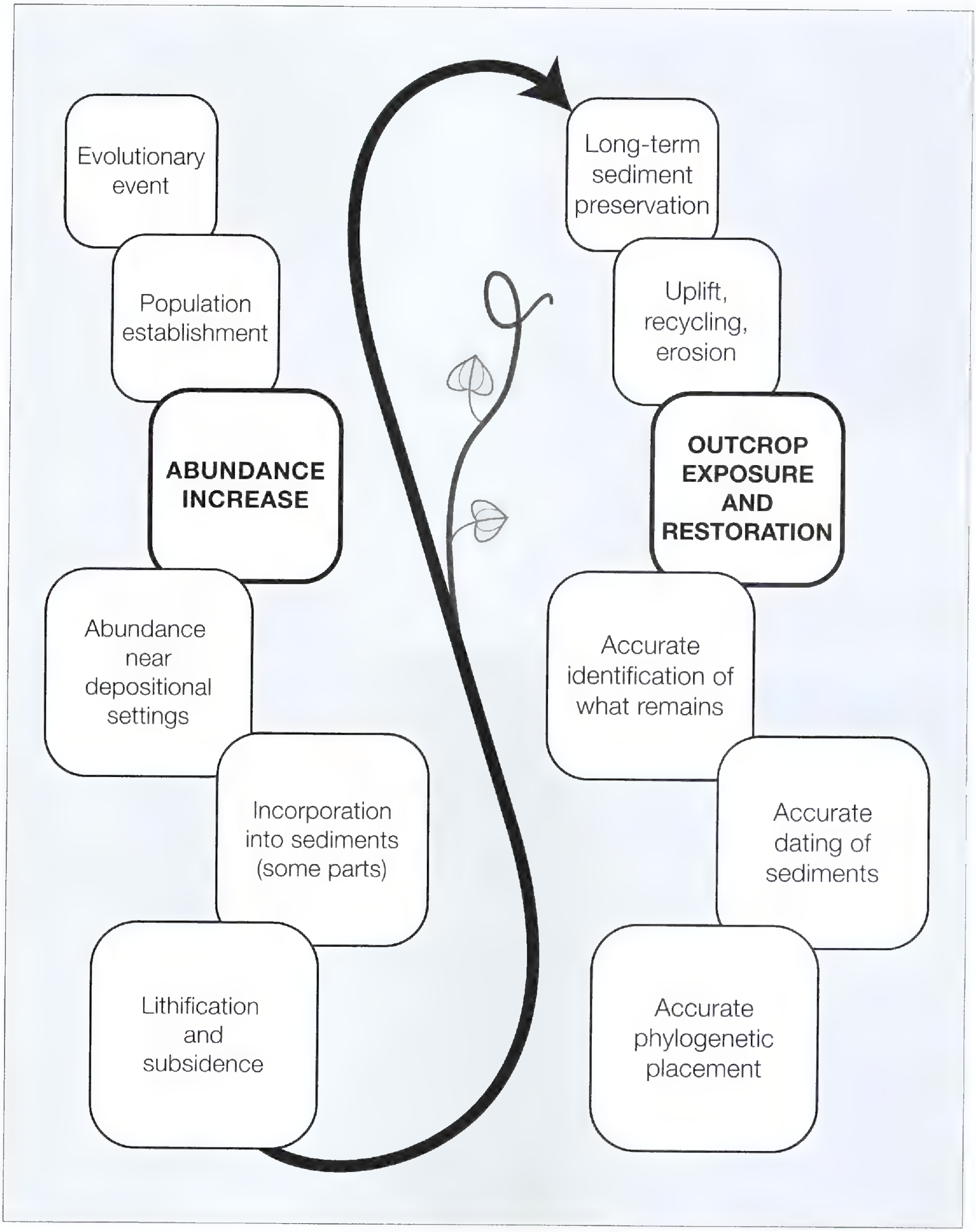
Evolutionary event
Population establishment
ABUNDANCE INCREASE
Abundance near depositional settings
Incorporation into sediments (some parts)
Lithification and subsidence
Long-term sediment preservation
Uplift, recycling, erosion
OUTCROP EXPOSURE AND RESTORATION
Accurate identification of what remains
Accurate dating of sediments
Accurate phylogenetic placement

Figure 1. Steps involved in fossilization of a newly evolved plant species. Each step involves some modification of the original plant form, population size and extent, abundance, or relationship to associated organisms.

tation in the fossil record? Then, several important steps are bypassed to address **outcrop exposure and exploration**, both of which are important in controlling the quality of interpretations made from the plant fossil record. This second step poses the question: are appropriate fossil-bearing deposits well represented and sufficiently studied in areas proposed as cradles of evolutionary events? A final note is added that opens the door on issues surrounding long-term sediment preservation.

STEP ONE: POPULATION EXPANSION AND MIGRATION. HOW LONG DOES IT TAKE FOR POPULATIONS TO EXPAND TO CONTRIBUTE TO THE FOSSIL RECORD?

Following the evolutionary establishment of a new plant species, it has been proposed that there is a substantial lag time before species have the potential to contribute to the fossil record, either because new species tend to be geographically restricted, or because they tend to be relatively rare in comparison to their longer-established relatives. This proposition, often linked to the idea of ghost lineages and added to (justifiable) suspected lack of taxonomic identification, is frequently cited in the plant evolution literature. This leads to the conclusion that the lag time between the evolution of the first angiosperm and its appearance in the fossil record can create an apparent explosion of angiosperm forms at its first appearance (Frohlich & Parker, 2000; Qiu et al., 2000). Interestingly, a gap in the record is rarely cited for the similarly radical innovations of grasses, where a more stately progression is generally easily described (Jacobs et al., 1999; Jacobs, 2004; Stromberg, 2004; Prasad et al., 2005). Although the lag time is rarely explicitly stated, for the explanation to fit the fossil record, the ecologically controlled lag times would need to be on the order of one to five million years to cause much discernable difference in analysis. Currently, this potential lag time is of critical importance in using fossil plants to date the appearance of higher-order clades (e.g., families, orders) and calibration of phylogenies based on molecular sequence data.

Although this argument has a great deal of potential validity, it has never been seriously tested using modern plant data from analogous evolutionary and ecological scenarios. Here, four ecological scenarios are examined in which expansion to large population sizes is used as a test of the lag time explanation for apparent gaps in the fossil record. The argument proposed is that if we evaluate settings under which plants colonize and expand, we can use the time required for colonization and expansion of large population sizes as a measure of the minimum lag time expected in the geological record. It is explicitly acknowledged that data are presented from success stories (i.e., species with capability for expansion, dispersal, and population longevity that may not be typical for the stem group of many plant groups). Therefore, data presented are the minimum time required for colonization and expansion of a newly evolved species. On the other hand, it could be argued that it is just those species with strong expansion capabilities that will ultimately form the stem group of a successful plant group. Either way, it is prudent to view these time frames as minimum estimates.

SCENARIO 1: POST-VOLCANIC COLONIZATION

Volcanic environments present a setting in which we can follow succession using a clearly defined starting date. Numerous volcanic eruptions over the past 1000 years are sufficiently studied to provide descriptive data on vegetative colonization. A massive eruption in Papua New Guinea (Long Island) is dated at 1645 and is estimated to be about the magnitude of the island volcanic eruption on well-known Krakatau. Some 350 years later, 273 species of seed plants, including 31 species of the genus *Ficus* L. alone, plus 32 pteridophytes are present (Harrison et al., 2001; Shanahan et al., 2001). Motmot, a caldera island established as a habitable island in 1968, had established *Ficus* seedlings within only three years of volcanic activity cessation (Shanahan et al., 2001). Even so, this level of recolonization is species-poor compared to the rich flora of nearby Papua New Guinea. The slow colonization has been attributed to the dry volcanic soils relative to the richer flora of Krakatau, which has a similar island setting and shorter eruptive history.

In comparison, the massive eruption in 1883 that destroyed vegetation (and habitations) on Krakatau left behind fertile ash soils in a humid tropical environment, both of which promoted rapid and diverse colonization. Only 100 years after the eruption, over 400 species had colonized (Whittaker et al., 1997), including some 100 species of climbing plants. Whittaker and colleagues propose that the island's flora is still disharmonic but "becoming less so" just 104 years following the devastation of the original vegetation (Whittaker et al., 1989; Bush et al., 1995; Thornton et al., 1996; Whittaker et al., 1997: 1671).

Volcanic environments can be rich in nutrients but relatively slow to accept colonizing species because the mantle of tephra and ash blankets the relatively more nutrient-rich debris flows and pre-volcanic soils. Because of high dispersal capabilities, ruderal species are generally the quickest to colonize (del Moral & Bliss, 1993). On Mount Lassen in California, forest trees may not have begun colonization until as much as 30 years after the cessation of eruptive activities (Kroh et al., 2000). Although colonization in volcanic environments can be slow, growth rates can accelerate once successful establishment has taken place, with many tree species reaching maturity within 20 years. On Mount St. Helens (Washington State, U.S.A.), interactions between site amelioration, dispersal ability, and colonizing ability prevent any concrete predictions on reassembly of communities (del Moral et al., 2005). However, species richness started to approach equivalence across all habitats surveyed by 20 years following the major eruption of 1980. In contrast, percentage cover was most rapidly increasing in safe sites and strongly ameliorated sites. Recovery of volcanic environments is clearly a slow process and is highly subject to the species attributes and environmental changes of the specific area. Vegetation recovery on Mount St. Helens 22 years after eruption indicates that stochastic processes are still in effect; deterministic processes have not yet taken over (del Moral & Lacher, 2005).

With relatively sparse data on long-term events in volcanic environments, we can still propose that in the absence of repeated events, even 2000 years should be sufficient for species in plant communities to expand to fossilizable population sizes. In the Neogene geological record of the western United States, it is clear that frequent disturbances can reset the ecological setting on long-term succession, as shown by Taggart and Cross (1990) for the Succor Creek and Trapper Creek floras.

SCENARIO 2: INVASIVE SPECIES INTRODUCTIONS

Another approach to estimating the rate at which new species can become abundant enough to contribute to the fossil record is to determine the rate at which introduced species spread across a new landscape. Knowing the date of the first documented arrival of a species (based on herbarium specimens, first cultivation dates, or vegetation surveys) provides a proxy for a new species origination. Literature on introduced and invasive species is reviewed here with the following question in mind: How long does it take to become a pest (common enough to become a fossil)?

Published literature is rich with reports of the impact and importance of invasive species, so this review is not intended to be exhaustive, but rather a sampling of life forms and phylogenetic diversity covered by the literature. In addition, summary ideas on invasive plants are extracted, relevant to the arguments here. Although attributes of species can help predict their propensity to be invasive, it is generally agreed that predictions are statistically based and individual cases are normally unpredictable (Kowarik, 1995; Rejmánek & Richardson, 1996; Williamson & Fitter, 1996; Kolar & Lodge, 2001; Hallet, 2006). A temporal framework for this discussion was provided by Usher (1988), who remarked that after 1000 years, it is virtually impossible to distinguish exotic from native plant species.

Based on intentionally imported species, a rule has been proposed that one of 10 species is likely to become naturalized once imported. Of those, one of 10 is likely to become a pest (Kowarik, 1995; Williamson & Fitter, 1996). Exceptions are important because crop plants are very likely to become naturalized (71 of 75 surveyed; Williamson & Fitter, 1996) and of 235 species introduced for horticulture, 82% have been found naturalizing outside of cultivation (Reichard, 1997). Still, the important step to pest status is quite low for crop species, yielding a one in 100 chance of rising to pest status for most imported crop species. Interestingly, this value is similar for Hawaiian plants (90 in 900 of naturalized invasive plants are threats to ecosystems; Loope, 1998), which have gained a great deal of attention because of their island setting.

An abbreviated list of invasive plants for which dates of introduction and approximate dates of pest status are readily available is presented in Table 1. This compilation does not include crop plants or plants that are only invasive in island ecosystems. Sampled are a range of life forms (trees, herbs, lianas, shrubs, aquatic plants) and a range of phylogenetic diversity (ferns, conifers, dicotyledonous angiosperms, and monocotyledonous angiosperms). At the species level, the results are astonishing because some introduced species rapidly rise to pest status. At a community-floristic level, Henry and Scott (1981) reported that 29% of the plant species in Illinois were documented aliens, and 13% of all woody species were aliens as of their study date. These figures are in line with figures reported from other preserved areas of the United States (Pimental et al., 2000: 26% in Great Smoky Mountain National Park; Yost, 1991: 36% alien to the New York State flora).

Table 1 suggests that if a species has a propensity to become abundant, it can rise to abundance in less than 500 years in almost all cases studied. There is a surprising amount of consensus on what combination of attributes most predispose introduced plant species to become invasive. Despite the statement by a National Academy Committee (Committee, 2002) that "The rate of immigration of plants and arthropods via *natural* [italics mine] means appears so low as to cause little concern about the arrival of detrimental species," it is likely that on a scale of 1000 years, this natural immigration would be of note. It is this longer scale we are concerned with here. Similarly, while plant traits are important, the complementary view that the disassociation of plants from their coevolved parasites and herbivores is also an important aspect of current plant invasiveness (Lake & Leishman, 2004; Hallett, 2006). Newly evolved species may have few parasites early in their evolutionary history, which would only add velocity to the rate of expansion. I emphasize here that the ecological literature clearly treats lag times as real and they certainly are so on an ecological time scale, but the time lags mentioned in the ecological literature are almost always less than 2000 years (Sakai et al., 2001; Crooks, 2005). In a particularly

Table 1. Examples of selected invasive species for which the following can be determined: place of origin, place of invasive record, time to recognized pest status, and literature source.

Genus and species	Family	Place of origin	Place of invasion (first appearance date)	Time to pest status (years)	Source(s)
Acer platanoides L.	Aceraceae	continental Europe and the Caucasus	MA, NJ, DE (introduced ca. 1775)	< 200	Webb & Kaunzinger, 1993
Schinus terebinthifolius Raddi	Anacardiaceae	South America (Brazil, Argentina, Paraguay)	Central America, Bahamas, Caribbean islands, FL, Mediterranean Europe, North and South Africa, China, South and Southeast Asia, Australia, Pacific islands (1832 or 1842–1849)	70	Morton, 1978; Ferriter, 1997; Williams et al., 2005
Vincetoxicum rossicum (Kleop.) Barbar.	Apocynaceae	Ukraine and Russia	northeastern and midwestern America (1890)	100	Sheeley & Raynal, 1996
Ambrosia artemisiifolia L.	Asteraceae	America	France (1865–1880; possibly 1681?)	15	Dessaint et al., 2005; Pederson et al., 2005
Solidago altissima L.	Asteraceae	North America	Europe (1750?)	250	Weber, 1998, 2001
Solidago canadensis L.	Asteraceae	North America	China (1935) to Shanghai	70	Weber, 2001; Dong et al., 2006a, b
Berberis thunbergii DC.	Berberidaceae	central and southern Japan	NJ to NH, west ND and SD; introduced to Arnold Arboretum (ca. 1870)	100	Ehrenfeld, 1997, 1999
Butomus umbellatus L.	Butomaceae	mainland Europe, U.K., Ireland, temperate western Asia	northeastern North America (1897)	< 100	Tutin et al., 1980; Brown & Eckert, 2005; Kliber & Eckert, 2005
Lonicera japonica Thunb.	Caprifoliaceae	Asia	eastern U.S.A. (ca. 1860)	< 125	Schierenbeck, 2004; Yates et al., 2004; Yurkonis & Meiners, 2004
Celastrus orbiculatus Thunb.	Celastraceae	southeastern Asia	eastern U.S.A. (1860)	90	McNab & Loftis, 2002; Ellsworth et al., 2004; Leicht & Silander, 2006
Bryonia alba L.	Cucurbitaceae	central and eastern Europe		50	Novak & Mack, 1995, 2000
Sphaeropteris cooperi (F. Muell.) R. M. Tryon [syn. *Cyathea cooperi* (F. Muell.) Domin.]	Cyatheaceae	Australia	HI (1950s)	40	Medeiros et al., 1992; Durand & Goldstein, 2001
Elaeagnus umbellata Thunb. ex Murray	Eleagnaceae	Japan, China, Korea	IL (and throughout the northeastern U.S.A.)	21	Ebinger, 1983; Yates et al., 2004
Sapium sebiferum (L.) Roxb.	Euphorbiaceae	subtropical China	GA (1772)	ca. 200	Bruce et al., 1997; Barrilleaux & Grace, 2000; Siemann & Rogers, 2001

Table 1. Continued.

Genus and species	Family	Place of origin	Place of invasion (first appearance date)	Time to pest status (years)	Source(s)
Pueraria lobata (Willd.) Ohwi	Fabaceae	Asia	Philadelphia, FL, southeastern U.S.A. (1876)	75	Miller & Edwards, 1982; Miller, 1985; Mitich, 2000; Pappert et al., 2000; Lembke, 2001
Lygodium microphyllum (Cav.) R. Br.	Lygodiaceae	tropical Southeast Asia, Africa, Australia	southern FL (1958)	20	Nauman & Austin, 1978; Pemberton & Ferriter, 1998; Dougherty, 2003; Lott et al., 2003; Volin et al., 2004
Syzygium jambos (L.) Alston	Myrtaceae	Southeast Asia	Puerto Rico (1821)	115	Brown et al., 2006
Psidium guajava L.	Myrtaceae	tropical America	Fiji, Namibia, Galapagos (1870)	120	Partridge, 1979
Pinus radiata D. Don	Pinaceae	North America, 4000 ha. on CA coast	Australia, South Africa, and New Zealand (1865), but large-scale planting in 1930	130 max., possibly only 60	Cronk & Fuller, 2001
Spartina alterniflora Loisel.	Poaceae	Gulf of Mexico, east coast of North America	WA (Willapa Bay) (ca. 1905)	90	Stiller & Denton, 1995; Davis, 2005
Polygonum perfoliatum (L.) L.	Polygonaceae	East Asia: Japan, Philippines	OR then PA (1890)	75	Reed, 1979; Oliver, 1996; Kumar, 2005
Rhamnus cathartica L.	Rhamnaceae	Europe	North America (1824)	ca. 100	Gourley, 1985; Heneghan et al., 2004
Paederia foetida L.	Rubiaceae	Japan	FL, NC, TX (ca. 1867)	50	Brown, 1992; Diamond, 1999; Flores, 2003
Salvinia molesta D. S. Mitch.	Salviniaceae	southeast Brazil	Kakadu Natl. Park, Australia; SC (1995); TX (1998); LA to NC (2000)	1	Cowie & Werner, 1993; Jacono & Pitman, 2001; McFarland et al., 2004
Selaginella kraussiana (Kuntze) A. Braun	Selaginellaceae	South Africa, Azores	Neotropics, southern U.S.A., Europe, New Zealand esp., HI, Norfolk Island, Waitakere (?) (1919, New Zealand)	< 80	Wilson, 1996; Roy et al., 2004
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	eastern and central China	U.S.A. (1784); Ontario, Canada (1998)	ca. 100	Meloche & Murphy, 2006

detailed review of lag times, Kowarik (1995) reported a time lag of about 147 years between introduction and invasive status among 182 species studied.

Characteristics commonly cited as beneficial to plants establishing expanding populations across a new habitat or continent, and thus potentially leaving an immediate fossil record, have been addressed frequently in the literature (Baker, 1974; Scott & Panetta, 1993; Pyšek et al., 1995; Rejmánek & Richardson, 1996; Reichard, 1997; Reichard & Hamilton, 1997; Clark et al., 2001; Kolar & Lodge, 2001; Sakai et al., 2001; Lake & Leishman, 2004; Richardson & Rejmánek, 2004; Rejmánek et al., 2005). From these, we can list attributes most likely to be found in plant species with the best potential for an immediate fossil record following evolutionary appearance as follows: vegetative reproduction, including forming thickets with high leaf area; large number of propagules produced and high consistency in production; small seeds and/or propagules with strong adaptations for vertebrate dispersal; short juvenile period; family or genus includes other invasives; broad ecological tolerance (via phenotypic plasticity and/or broad latitudinal range). Species of fossil plants most likely to bear these characteristics are the best candidates for use in reconstructions and paleoclimatic and phylogenetic studies.

SCENARIO 3: SUCCESSIONAL FOREST AND REGENERATION RATES

A third strategy for estimating the rate of expansion of new species is to examine records of regenerating forests in temperate and tropical landscapes. Forests that have been clear-cut for ranching, lumbering, or mining, or devastated by landslides or hurricane winds are ideal settings for estimating rates of regeneration of populations to abundances that can contribute to the fossil record. This scenario is treated here separately from that of volcanic settings largely because of a more rapid rate of regeneration due to plant root and stem stocks and the smaller geographic extent of destruction expected. The two scenarios overlap to some degree.

Again, the literature is rich in case studies of forest regeneration. Only a few of the many studies from temperate, subtropical, and tropical climates are selected for estimation of regeneration rates. This summary is restricted also to the regeneration of woody species, which are the most likely modern analogs to contributors to the fossil record (Ferguson, 1985; Burnham, 1997).

In Neotropical lowland sites (either maritime-influenced or wholly continental), the time of regeneration for heavily disturbed or damaged forests is on the order of 100–400 years (Guariguata & Ostertag, 2001) and even less when disturbance is short or less intense (Table 2). Several authors point to the importance of assessing forest recovery in terms of species composition, basal area, and forest function, rather than simply species richness (e.g., Guariguata & Ostertag, 2001). Accurate data on forest regeneration as much as 200 years after disturbance are very rare, so estimates are often made either by comparison among different-aged forest disturbances or by extrapolation from single forests from much shorter time intervals. A direct assessment of forest regeneration could increase the average time of recovery well beyond 400 years, but it is unlikely that it would extend it as much as one order of magnitude to 4000 years. Significantly, repeated and continual disturbance suppresses total forest regeneration as shown by Rico-Gray and Garcia-Franko (1992) in forests in Yucatán, Mexico. A review of the successional literature for the Neotropics published in 2001 was characteristically noncommittal on any maximum rate of forest regeneration but acknowledged that "the regenerative power of neotropical forests vegetation is clearly high" (Guariguata & Ostertag, 2001: 185).

In temperate forests, data on human clearing are more readily available and can be used as the forest destruction date. In these forests, similar results seem to apply: regeneration is on the order of 100–500 years (Table 2). Regeneration time is potentially longer under continued anthropogenic disturbance. In a review of temperate regeneration under large-scale disturbances, Turner et al. (1998) indicate that distance for dispersal and random processes (lack of predictable competitive hierarchies) are likely to apply but, again, over time scales that are not explicitly stated. Most authors report studies from relatively short time intervals, so their reluctance to commit to full regeneration is understandable. The combination of approaches mentioned below under Scenario 4 (migration rates) adds a dimension improving interpretations of these shorter-scale results.

This brief summary of the literature on regeneration in forested ecosystems in a variety of climates indicates that, again, plant species can and do expand to large populations in remarkably short periods of time, geologically. It would be surprising to detect any gap in the fossil record longer than 1000 years due to a single destructive event. Models of forest succession based on observations in the temperate zone generally employ time periods substantially less than that (e.g., Busing, 1995).

SCENARIO 4: MIGRATION EXPANSION RATES BASED ON FOSSIL POLLEN LINKED TO HISTORICAL RECORDS

The fourth approach taken here is to apply evidence from pollen in sediments to estimate rates of plant

Table 2. Selected studies indicating woody species' composition time to recovery in tropical and temperate forests (including one bog), ordered north to south.

Site	Climate	Recovery time (yr.): woody species	Type of disturbance	Source(s)
Sweden	temperate ombrotrophic peat mire	> 50	peat harvesting 50 yr. before abandonment	Soro et al., 1999
Boundary Waters Canoe Area (MN), U.S.A.	temperate moist forest	60 yr. for demographic transitions	dramatically reduced fire regimes; 57 yr. of direct observation	Frelich & Reich, 1995
Bolleswood Natural Area (CT), U.S.A.	temperate moist forest	> 50	post-agricultural	Fike & Niering, 1999
Fernow Experimental Forest (WV), U.S.A.	temperate mountainous forest	Structurally similar but unrestored after 100 yr.	logging, followed 20 yr. later by *Castanea* blight	Schuler & Gillespie, 2000
Great Smoky Mountains (TN), U.S.A.	temperate moist forest	ca. 200	abandoned agricultural fields	Clebsch & Busing, 1989
Great Smoky Mountains (NC/TN), U.S.A.	temperate	50–200	small natural gaps	Runkle, 1985
Yucatán, Mexico	lowland dry tropical	much more than 26 (forest not recovered at publication)	agave cultivation	Mizrahi et al., 1997
Dominican Republic	tropical maritime	40	60 yr. of agriculture	Martin et al., 2004
Puerto Rico	tropical maritime	40 (similar to > 80-year-old forest)	abandoned pastures	Aide et al., 1996, 2000
Luquillo, Puerto Rico	tropical maritime	< 100	human clearing and hurricane disturbance	Foster et al., 1999
Sarapiqui, Costa Rica	tropical lowland wet forest	ca. 150: dominants regenerated reach large sizes	5–10 yr. of pasture before abandonment	Guariguata et al., 1997
La Selva, Costa Rica	tropical lowland moist forest	< 440 (longest tree lifespan)	undisturbed forest	Lieberman & Lieberman, 1987
Tropical summary: Nigeria to Thailand to Venezuela	lowland secondary forests	average 80 (75–150)	human disturbance	Brown & Lugo, 1990
Barro Colorado Island, Panama	tropical lowland	50–100	natural river meanders	Knight, 1975; Dewalt et al., 2000; Denslow & Guzman, 2000
Colombia, Venezuela, Upper Río Negro	tropical continental	ca. 80–200	2–3 yr. of intensive agriculture on poor soil	Saldarriaga et al., 1988
Gran Pajonal, Peru	montane tropical rainforest	35 yr. to ca. 300 metric tons; uncut control ca. 600 metric tons	light pasture, 0–3 yr. of crop cultivation	Scott, 1977

species expansion from nascent populations to populations large enough to be recovered in the fossil record. Pollen deposited in lake, pond, estuary, or riverine sediments documents the presence of species in the catchment area. First appearances of plant invaders are used as a proxy for species evolution and employed in combination with historical exploration and land use records to give a minimum estimate for definite representation in the fossil record (at least in wetland areas). Similar to other approaches used here, pollen evidence is a best-case scenario resulting in the most rapid rates. The evidence presented overestimates the appearance in the fossil record of slow-moving taxa or taxa whose pollen is poorly represented in sediments. In addition, pollen is likely to be the first plant organ potentially recognized in sediments but is only rarely diagnostic to species (but see recent advances in Finkelstein et al., 2006). Pollen evidence overestimates the rate at which an average species can spread and be recognized in the fossil record.

Crawford Lake (southern Ontario) is a well-known example of pollen records including Native American and European colonizers (McAndrews, 1988; Jackson, 1997). Records indicate that with the expansion of Native Americans using small-scale cultivation methods, species that are known to favor disturbed habitats, such as *Portulaca oleracea* L. and *Zea mays* L., appeared and expanded. Evidence from a variety of sites (Easter Island; Lindsley Pond, Connecticut) was reviewed by Jackson (1997) and the obvious point is that the appearance of pollen of an invasive or introduced species in sediments is often interpreted as synchronous with the arrival of colonizing humans. This interpretation, while certainly not absolutely accurate, is widespread (Whitehead & Sheehan, 1985) and underscores the speed with which introduced species spread on arrival. Jackson (1997) summarized the rate of spatial expansion being on the order of tens to thousands of kilometers within 5000 years for entire plant communities. Synchronous invasions by *Tsuga* (Endl.) Carrière into several *Pinus* L. forests in North America are documented (Davis et al., 1998), evidence of invasions that appear to have taken place over less than 1000 years. Woods and Davis (1989) document range expansions over periods of 500–2000 years for *Fagus* L. Quite appropriately, data for *Fagus* and *Acer* L. were revisited using the distribution of genetic polymorphisms (McLachlan et al., 2005), showing that rates may not have been as rapid as some have envisioned. While the molecular estimates double the previously accepted migration rates of forest trees, even this doubling of migration rates suggests no major temporal gap between the appearance of new species and their recognition in the fossil record for the majority of the fossil record.

These four approaches to estimating the rate of species expansion following establishment support the idea that it is unlikely that gaps in the fossil record can be explained by an intrinsic lag in population establishment and expansion. Plant species appear to be able to both increase in population size and migrate to almost any area inhabitable by the species on the earth. Data are based on rapidly migrating, expandable species, but there is no intrinsic geological lag due to lack of colonizing or dispersal abilities. Time lags of as much as 2000 years may be expected for some species prior to establishment of large populations, contributing to the fossil record. However, this is not a long period of time relative to the acuity of the fossil record and is particularly short relative to the phylogenetic and morpho-developmental questions applied correctly. It is not likely, therefore, that the rate of species expansion is responsible for observed gaps in the fossil record itself or disharmonic results between molecularly based phylogenies and the sequence of appearance of taxa in the fossil record. Instead, observed or perceived gaps must be explained by other mechanisms, of which there are many.

STEP TWO: OUTCROP EXPOSURE AND EXPLORATION. CAN THE POTENTIAL FOSSIL RECORD PROVIDE ANSWERS?

The sequence of events leading from species origination to recognition and application of plant fossils includes a step that receives little attention: the potential for discovery of fossil-bearing outcrops and recognition of taxa represented (Fig. 1). This aspect of our understanding of earth's history has received remarkably little direct attention in the past, giving us little hard data with which to estimate the potential error in stratigraphic ages or global distributions. Because my interests have focused on fossil plants from northern South America (Burnham & Graham, 1999; Burnham & Johnson, 2004), I cover this topic in some detail here for relatively young sediments (Cretaceous to Pliocene) in northern South America. The topic deserves much more attention and could be profitably covered continent by continent by specialists. Two questions are addressed using data derived from Cretaceous- through Pliocene-age sediments from literature and accumulated outcrop data: (1) Is the quality of the published fossil record sufficient for constraining the timing of evolutionary events in northern South America? (2) If we knew every plant fossil deposited in every accessible outcrop in northern South America, would that be sufficient for dating phylogenetic trees, mapping past ecological or geographic distributions, or documenting a complete sequence of evolutionary events?

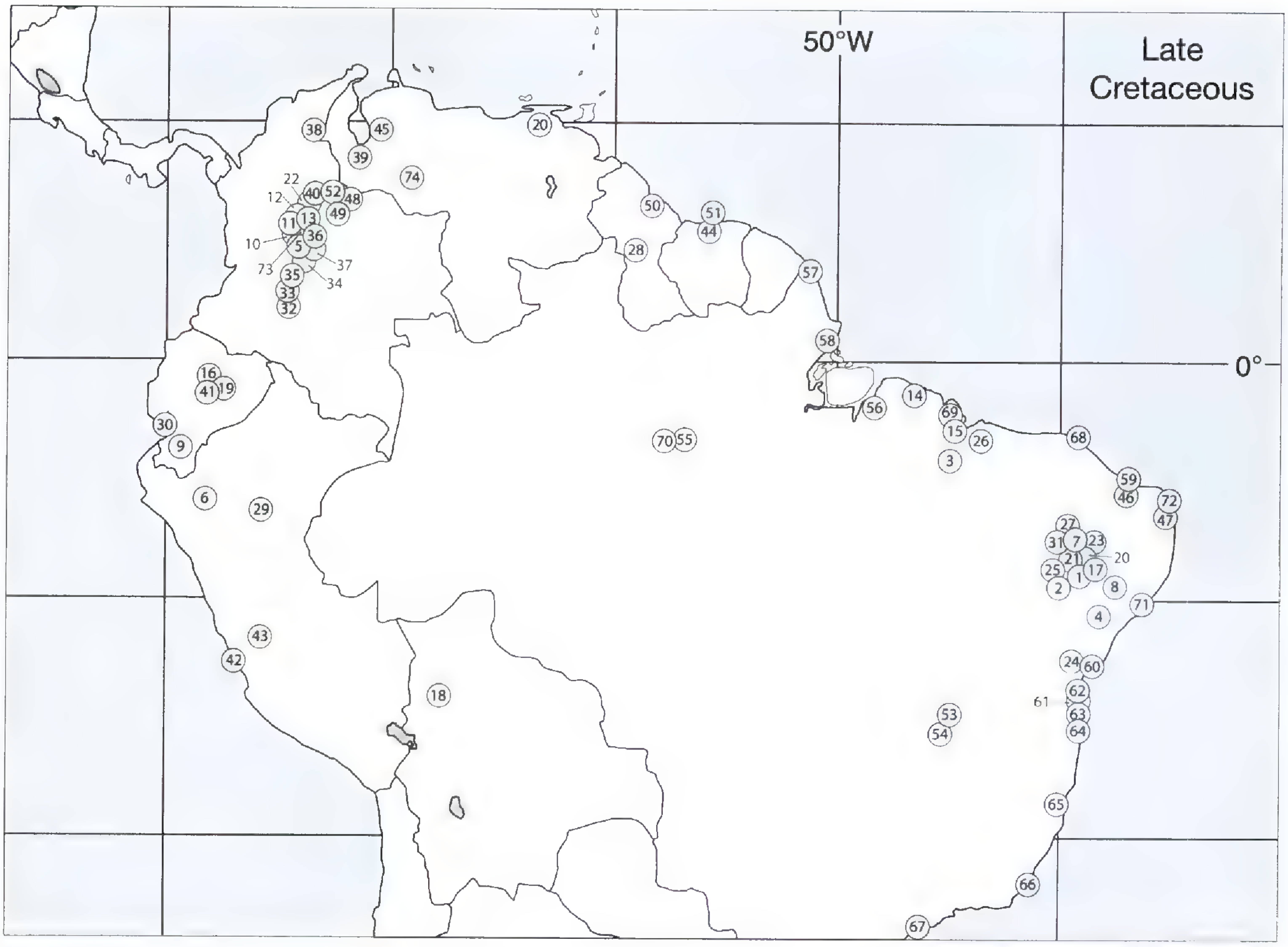

Figure 2. Known late Early and Late Cretaceous–age plant fossil localities in northern South America as of December 2006. Data for localities were extracted from the literature, with each site numbered in a database available from the author. Localities included from Aptian to Maastrichtian.

THE QUALITY OF THE PUBLISHED PLANT FOSSIL RECORD

In 1999, Burnham and Graham published a series of five maps of northern South America, plotting all fossil plant localities known to us from the Late Cretaceous, Paleogene, Miocene, Pliocene, and Quaternary. Collectively, the data appeared rich (Burnham & Graham, 1999: fig. 2), but the 243 fossil localities were scattered over more than 80 million years and over 13,000,000 km^2; thus, the number of localities per time unit or per unit area was really quite small, even compared to our limited understanding of the distribution of modern biodiversity. Moreover, more than a quarter of those localities (28%) represented Quaternary sediments, a tiny fraction (roughly 2%) of the 80 million years of sediment surveyed. In 2006, a resurvey of the paleobotanical and geological literature, published Internet sites, and more complete bibliographic searches turned up a much larger number of sites for each time period evaluated, in addition to seven years of added publication activity (see Table 3). Updated maps are published here for the Late Cretaceous, Paleogene (three subintervals included), Miocene, and Pliocene (Figs. 2–5). Quaternary deposits were not resurveyed in 2006. A total of 332 pre-Quaternary localities are now known (compared to 174 pre-Quaternary localities known in 1999). A comparison of these data sets is presented here as Table 3. Significant in both data sets and from inspection of both series of maps (Figs. 2–5) is the paucity of known plant localities from the Amazon Basin for more than 80 million years (Late Cretaceous through Pliocene; see also Burnham & Graham, 1999; Figs. 2–5). The rocks of the Amazon Basin are complex, and, yet, a large proportion is mapped either as igneous and metamorphic rocks of Precambrian age, or as Pliocene- and Quaternary-age sediments blanketing an unknown base (SIG, 2002). Many of the known fossil plant localities are sediment cores, which typically can only provide palynological data. However, in parts of the Brazilian Amazon, rocks of Cenozoic or Cretaceous age are mapped but poorly studied. These areas represent the sites of greatest changes in density of localities between the 1999 and 2006 surveys of localities, but the large extent of rock that could potentially contribute to the plant fossil record has been underexplored. Improvements on the

Table 3. Comparison of locality numbers per geological period for two literature census dates. Because literature was combed more deeply for the Cretaceous localities in the 2006 survey, the two Cretaceous values differ not only because of the addition of Aptian and Albian localities in the 2006 census, but also because of intensified publication activity and better searching techniques (search engines, online libraries, and software) in 2006. my = million years.

Geological period	Approximate duration (my)	Localities presented in 1999	Localities presented in 2006
Quaternary	1.8	69	Not censused
Pliocene	3.5	35	38
Miocene	18	75	116
Oligocene	10	18	37
Eocene	22	27	44
Paleocene	10	6	23
Late Cretaceous	35 (1999)	13	74
	55 (2006)	Cenomanian to Maastrichtian	Aptian to Maastrichtian
Total localities		174	332
		243: including Quaternary	

known fossil locality maps Burnham and Graham published in 1999 give us hope that further explorations, with this more complete set of known localities, will help close the gaps where they yawn the widest.

The number of fossil data points that contribute to dating recent land plant phylogenies based on molecular evidence is remarkably small and yet is drawn from global sources (Fishbein et al., 2001; Conti et al., 2002; Bremer et al., 2004; Davis et al., 2005; Crayn et al., 2006). South America has the potential to contribute substantially, as demonstrated by the spectacular fossils of early angiosperms and gnetaleans recovered from the Crato Formation in Brazil (Mohr & Eklund, 2003; Rydin et al., 2003) and the diverse angiosperms reported from the Paleocene and Eocene from Colombia (Jaramillo, 2002; Jaramillo et al., 2006) as well as from the Miocene of Ecuador (Burnham, 1995; Burnham & Carranco, 2004; Burnham, unpublished). However, much of the Late Cretaceous and Cenozoic sedimentary rock that is known to exist in South America has not been adequately explored to determine whether it bears fossil plants, much less sustained detailed taxonomic studies. For example, a large expanse of Cretaceous sediment is evident from maps of the adjoining states of Goias, Tocantins, and Bahia, Brazil, but I have not yet found a single reference to fossil plants from this area. Similarly, the geologic map of Bolivia bears indications of appropriately aged sediments, and, yet, this country consistently shows few localities on each of the 2006 maps presented here. These specific examples underscore the importance of gaps in our knowledge of the potentially available fossil record, in contrast to gaps that may be created by lack of deposition, lack of preservation, or erosion of fossiliferous sediments prior to discovery. Some gaps might be filled by data that are still held as proprietary by commercial concerns (oil, gas, and other mining exploration).

The impact of gaps on applications of the fossil record to paleogeography, paleoclimate, phylogenetics, and even ecosystem change is extreme. For example, due to the limited subset of fossil calibration points for phylogenetic trees, the same data can be used to constrain timing for alternative scenarios of plant evolution. Drastically different scenarios can be equally plausible if calibration points are few, or are biased toward specific regions of the world. Similarly, data on paleoclimatic parameters based on fossil plants are limited by known localities that can be analyzed for such data. A single fossil assemblage from a small area can be assumed to be representative of a large geographic area (as is generally assumed), but it can also be atypical, representing a low moist area in a surrounding nondepositional, dry area (Burnham et al., 2001; Kowalski & Dilcher, 2003). Interpolation of paleoclimatic points between sites that are more closely spaced is obviously preferred. Lack of intensive collection and documentation of fossils in certain geographic areas will severely bias paleogeographic reconstructions of species distributions.

In contrast to the promising results from the first step of the fossilization process presented here (Abundance Increase; Fig. 1), in some parts of the world and for some time periods, the fossil record should be read very cautiously. Presence of a taxon in the fossil record is a known anchor for evolutionary events, but such data cannot be used to weight particular areas or time periods if sufficient geological and paleobotanical exploration has not been carried out elsewhere (see, for example, the distribution of localities in fig. 2 of Gingerich, 2006). A recent

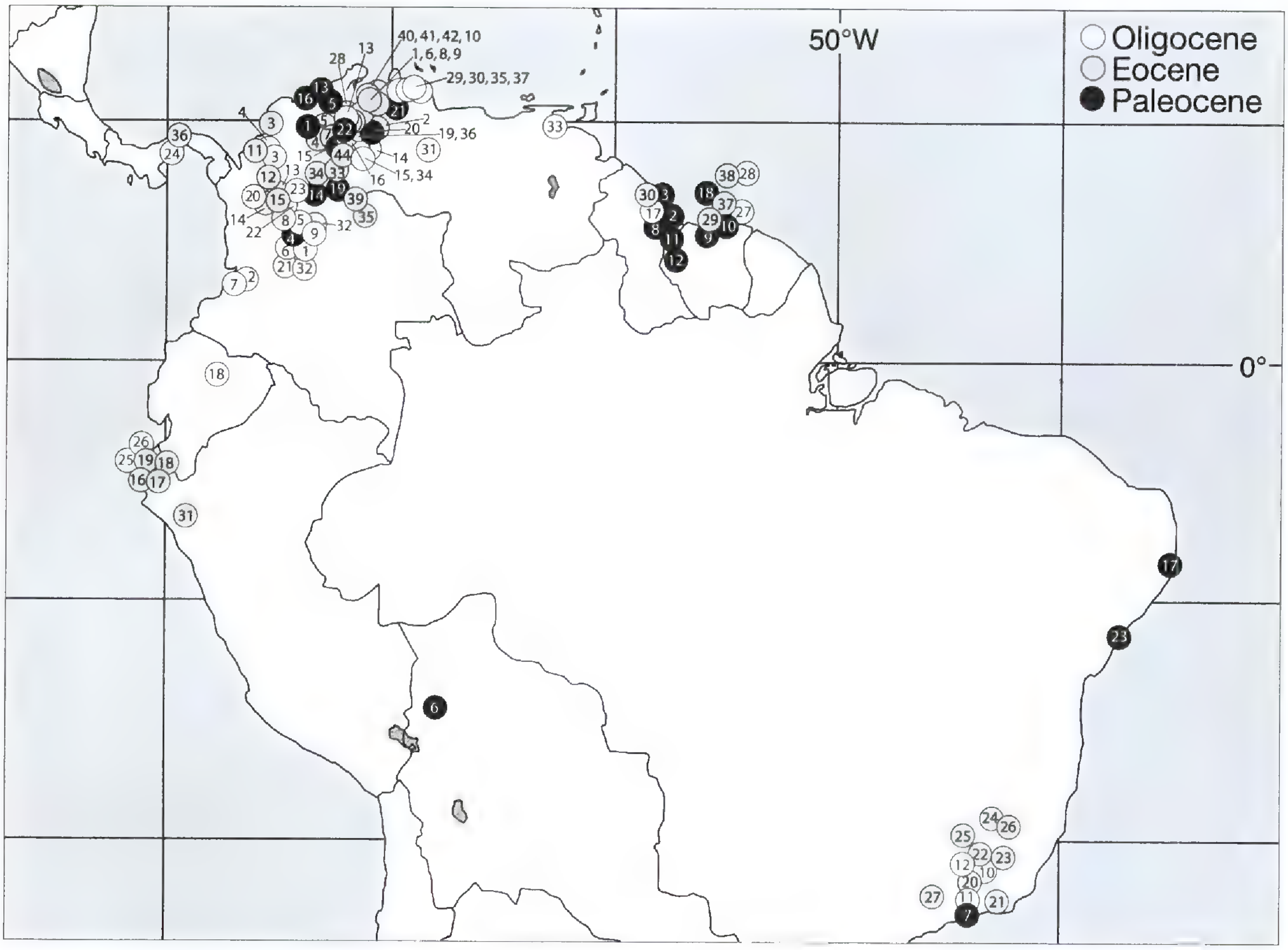

Figure 3. Known Paleogene-age plant fossil localities in northern South America as of December 2006. Data for localities were extracted from the literature, with each site numbered in a database available from the author. Localities are coded to show age assignment to Paleocene, Eocene, or Oligocene.

extensive review of the Malvoid pollen record (Krutzsch, 2004) proposed evolutionary and migration scenarios based on worldwide pollen records. While the review is complete in terms of published information, we have to wonder how much of the scenarios might be altered with just two additional records of Malvoid pollen from South America. The absence of evidence in unexplored areas needs to be recognized as just that.

Can the Potential Fossil Record Answer Our Questions?

The second question posed above is potentially unanswerable because of our lack of understanding of global depositional patterns over time: if we knew the identity and morphology of every fossil deposited in every accessible outcrop, would that be sufficient for confirming the validity of dates for phylogenetic trees or for confirming evolutionary events?

While we can more intensively sample areas of the earth that are poorly represented by fossils of particular taxonomic groups and ages (addressed in the preceding paragraphs), a more substantial issue lurks within the deposition and preservation of the sedimentary rock record itself. Ronov and colleagues (Ronov et al., 1979, 1980; Ronov, 1994) painstakingly measured the area of rock outcrop for epochs over the past 543 million years. These monumental efforts were hampered at the time by the same kinds of gaps in our knowledge of surficial geology in remote areas that we have today. Nevertheless, the work demonstrated (Ronov et al., 1980) that within each geological period from the Lower Permian to the present, the proportion of rock volume composed of coal-bearing rocks (the most likely to preserve plant fossils) is between 0.3% and 8.1% (a high of 11.2% is recorded in the Carboniferous period). If we add all other sedimentary rocks that could potentially incorporate plant remains (but probably do not, such as coarser river sediments) to those coal-bearing sediments, we get a maximum of 16%–30% of the rocks preserved from any geological period, which have the potential to bear identifiable plant remains. Of course this is highly variable, temporally.

This result is sobering because this may mean that mapped geological exposures of any specified time period have, on average, less than a 30% chance of

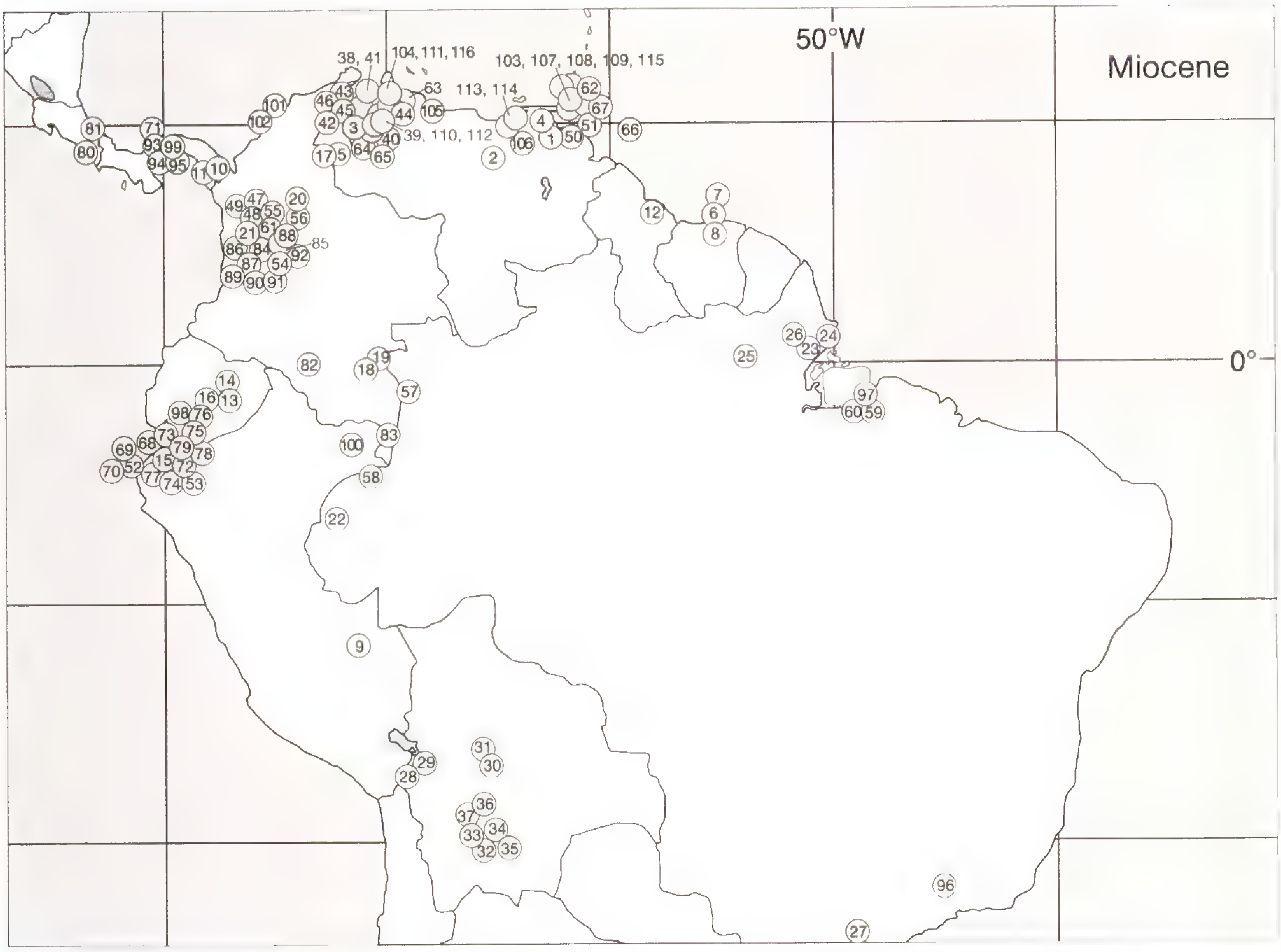

Figure 4. Known Miocene-age plant fossil localities in northern South America as of December 2006. Data for localities were extracted from the literature, with each site numbered in a database available from the author.

yielding rocks that potentially bear plant remains. What is of even more concern is a concept recently cogently explained by Peters (2005) that the potential for sedimentary deposition *and* preservation is strongly controlled by continental position and, in particular, sea-level change. Peters (2005, 2006) employed the COSUNA (Correlation of Stratigraphic Units of North America) charts, which are based on some of the most well-known terrestrial and marine sedimentary sequences in the world. He asked the question: Is the temporal continuity of sedimentary rock over time correlated with either first or last appearances of taxa (in his case, genera), thus indicating that the two are not mechanistically independent? He showed that, in fact, almost every aspect of temporal variation in the fossil record is reflected in similar variation in the spatial and temporal distribution of sedimentary rocks. In his work, Peters (2006) also demonstrated that the total volume of terrestrial sedimentary units over North America increased dramatically over the last 90 million years. This increase in all sediments in the recent geological past is overprinted on extreme variability in the proportion of sedimentary packages constituted by fine-grained sediments (ideal for fossil plant preservation) over time. The presence of multiple marginal depositional basins is correlated with a high potential for sedimentary accumulation. An increase in sediment accumulation logically occurs when plate tectonic configurations are such that they accommodate the formation of large sedimentary basins. One implication of this result is that we should expect to find that many plant fossils appear synchronously in the fossil record, not for evolutionary reasons, but as a result of tectonic forcing of the sedimentary record. Peters' data would suggest that interpreting first occurrences as true originations is likely to be erroneous, given that the preservation potential is so much higher when tectonic plate configurations foster the accumulation of fine-grained sediments. One specific geographic location where this might have had a strong effect is in the eastern portion of Brazil, where well-preserved plant remains uniquely represent early angiosperms and gnetaleans. However, this was just the kind of tectonic setting where deposition would be predicted. So were angiosperms and gnetaleans living there preferentially, or are they simply preserved preferentially there?

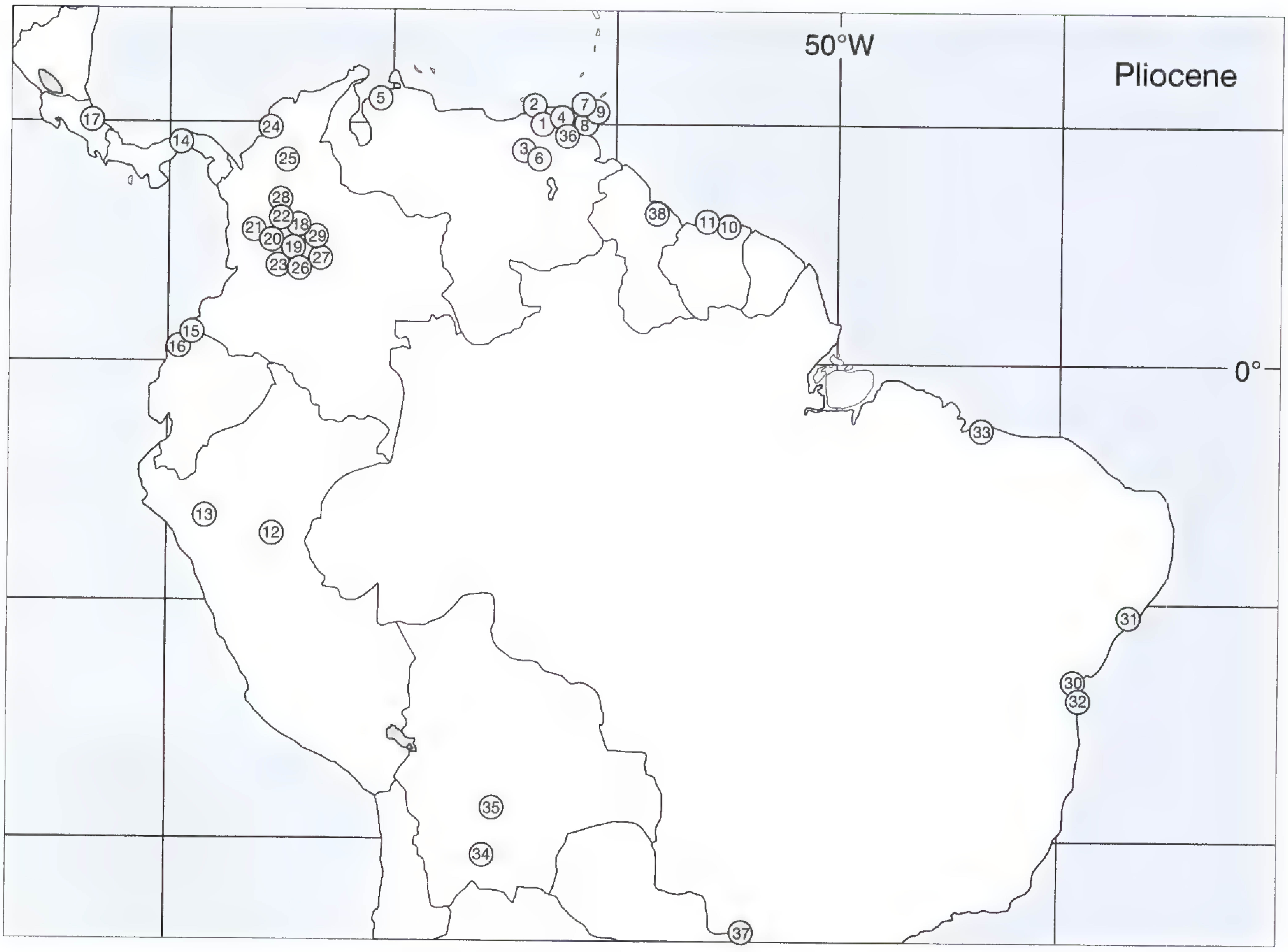

Figure 5. Known Pliocene-age plant fossil localities in northern South America as of December 2006. Data for localities were extracted from the literature, with each site numbered in a database available from the author.

While this evidence might be far from the minds of those involved in phylogenetic analysis and the application of fossil plant data to constraining evolutionary scenarios, it is critical to recognize that the fossil record is both preserved and subsequently sampled in a highly nonrandom manner. Overriding considerations are the completeness of the record of any one time period, the depositional circumstances under which the original data were preserved, and the erosional circumstances of the intervening time period between deposition and exhumation.

In conclusion, this contribution addresses two important steps in fossilization and recovery that apply to a wide variety of paleobiological and evolutionary questions. Four scenarios are provided under which it can be seen that plant populations grow rapidly from a very small number of individuals to populations large enough to contribute substantively to the fossil record in a geologically short period of time (ca. 2000 years). This period of time may not be resolvable in the rock record and, as such, can be thought of as instantaneous. Migration rates of plants are generally rapid enough that there is no discernable lag time that would be produced in a fossil record if a successful plant or plant group is to be anticipated to migrate over large land areas. These data apply only to the rock record prior to the Quaternary, in which resolution is not expected on these ecological scales. Most of the modern analogies I have used to address this question are based on successful immigrants or invasives, and some are expanding under circumstances of lowered competition and predation. Therefore, the quantitative data here are recognized as representing the short end of the time-to-expansion spectrum. It is not possible to give estimates of expansion rates for a given fossil species if reproductive intervals, time to reproduction, or even ability to vegetatively reproduce are unknown for that species. Instead, it is reasonable to assume that a plant group that ultimately does contribute substantively to plant diversity, density, or vegetational importance (defined as many species within the group, biomes dominated by members of the group, continent-wide coverage by members of the group) has done well at some time in its evolutionary history, and the time scale of expansion of 10–1000 years is applicable.

In contrast, the recovery of a high-quality fossil record depends on a number of factors that are not as easily dismissed. We should be especially cautious in assuming the adequacy of the currently known and potentially retrievable fossil record in answering detailed questions about plant evolution. While the rock record is incomplete, the analysis does not need to stop there. If the fossil record can be quantified both globally and regionally relative to the probability of bearing and preserving fossil plants, we would be able to assign confidence limits on the presences and absences that are applied from the rock record. Approaches like this have been carried out on pure sedimentary gap analysis and for paleobiodiversity analyses (see papers by Sadler & Strauss, 1989, 1990; Holland, 2000; Crampton et al., 2006) and hold great promise for the geographic and stratigraphic absences of fossil plants.

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